

NORMANICYTHERE GEN. NOV. (PLEISTOCENE AND RECENT) AND THE DIVISION OF THE OSTRACOD FAMILY TRACHYLEBERIDIDAE

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ABSTRACT. Taxonomic criteria are examined and a review of the family Trachyleberididae leads to a revised diagnosis of the subfamily Hemicytherinae. One of Norman's specimens is designated lectotype of *Normanicythere leioderma*, the type species of the new genus. The lectotype and a number of syntypes are figured for the first time, together with fossil Pleistocene material. Changes of hinge structure during development are described. The affinities of the genus are discussed and its growth and distribution examined.

INTRODUCTION

Cythere leioderma was first described by the Rev. A. M. Norman (1869, p. 291) from Recent material dredged from 'very deep water in Unst Haaf' in the Shetlands in 1867. These nine specimens, which were never figured, are in the British Museum (Natural History). Brady published the first figures of the species (1870, pl. 19, figs. 11-13) showing a complete female shell seen from the left (fig. 11), above (fig. 12), and behind (fig. 13). This came from the Gulf of St. Lawrence, Canada, where he records this as being the most abundant species in the Canadian dredgings (although the Canadian workers inform me that they have no knowledge of it). From his figures and description Brady's interpretation of the species would seem to be valid enough although the material on which it was based has so far not been traced, and even though at that time he had not seen Norman's type material for he mentions 'the single (?) specimen described by Mr. Norman' (Brady 1870, p. 452). The main features on which recognition of the species was based seem to have been the general shape of the shell, the smooth unsculptured surface, and particularly the 'few very distant punctured papillae' (Norman 1869, p. 291). Brady comments that this latter is probably an optical illusion (1870, p. 451) and Brady and Norman (1889, p. 139) agree that there are a 'few scattered, short and rigid setae, which in some lights look deceptively like small circular papillae'. These early authors do not mention the muscle scar pattern or soft parts and their description of the hinge is confined to generalities. Thus Norman in his original description says 'This species has much more the aspect of a *Cytheridea* than of a *Cythere*, but the hinge margin is not toothed', while Brady, Crosskey, and Robertson (1874, p. 149) note 'hinge teeth strongly developed' and Brady and Norman (1889, p. 139) say 'Hinge . . . processes very strongly developed but not crenulated'.

The only published figure giving a reasonable representation of the adult hinge, and then only in dorsal view, is the male right valve figured by Brady, Crosskey, and Robertson (1874, pl. 9, fig. 6). Müller (1912, p. 377; 1931, p. 30) referred to this species under 'Genera dubia et species dubiae Cytheridarum', and Elofson (1941, p. 304) also had difficulty in placing *C. leioderma* systematically, referring it very doubtfully to *Cythereis*. On the other hand, Blake (1933, p. 239) stated that 'In spite of the remarkable form of the shell, the hinge and appendages show this to be a normal species of *Cythereis*'. Blake, however, took a very wide definition of the genus *Cythereis* even for 1933, and [Palaeontology, Vol. 2, Part 1, 1959, pp. 72-93, pls. 13-14.]

reduced *Hemicythere* to the status of a subgenus of the former. In view of the large amount of work done on '*Cythereis*' in the past two decades Blake's comments on the hinge now read rather strangely and the soft parts need re-examination. Specimens showing the soft parts are rare and this is the only allusion to them in the whole literature. Blake's specimens are no longer available for study since the material has been disbanded and is now untraceable.

It is doubtful whether it will ever be possible to define the nature of the soft parts in *Cythereis* s.s. as the type species is a Cretaceous form, although recent techniques developed by Martin (1957) perhaps hold out some slight hope here for the chitinized parts of the animal. The selection of *Cythereis montereyensis* by Skogsberg (1928, p. 9) as the type species for *Cythereis* s.s. is invalid since this is not one of the original species included in *Cythere* (*Cythereis*) by Jones (1849), a point made by Blake (1933, p. 238). Triebel (1940, p. 174), in making *Cytherina ciliata* Reuss 1845 the type species, was the first to select a valid type for the genus, and both his diagnosis, and the later one in English by Sylvester-Bradley (1948, p. 795), show that the hinge of the type differs radically from that of the present species. This is particularly obvious in the case of the right valve where the latter has a stirpate anterior tooth and a reniform posterior tooth while *Cythereis* has dentate anterior and posterior elements.

During an examination of the Pleistocene Sub-Basement Clay at Dimlington on the Yorkshire coast (see Bisat 1939*a, b*; 1954 for stratigraphical details) three specimens were obtained and showed a number of interesting features, particularly in the development of the adult hinge structure. These features are paralleled in Norman's type material and are here described for the first time. Hitherto the only figured specimen from this country was the single adult valve noted above from the Bridlington Crag (see Phillips 1875, pp. 86, 163, for stratigraphical details). The new Dimlington material, Norman's type specimens and the three previously unrecorded valves in the Hancock Museum, Newcastle, together with the abundant and excellently preserved Spitzbergen material, now make it possible to describe and figure this species adequately for the first time.

GENERIC CRITERIA

It is a truism that the different approaches of the zoologist and palaeontologist to the problems of taxonomy are governed by the nature of the material available, and that discrimination of fossil species and genera must always be to some extent subjective. The zoologist naturally attaches most importance to the soft parts of the living animal and, in the case of the Ostracoda, bases his differentiation particularly on the nature of the limbs and genitalia. This is abundantly clear in Skogsberg's work (1928) on the genus *Cythereis* for he records (p. 12) that 'the structure of the mandible is, indeed, the most characteristic feature of the genus *Cythereis*' and goes on to state (p. 16) that 'a subdivision of the genus *Cythereis* on the basis of the shape and structure of the shell is, generally speaking impossible. . . . The subdivisions must, on the contrary, be based on the structure of the appendages and of the penis. Especially the structure of the penis appears to be significant.' Blake (1933, p. 238) reiterates this view that a knowledge of the appendages is necessary for the discrimination of subgenera in *Cythereis*. He goes on to note that in *C. leioderma* the hinge is that typical of *Cythereis*—a statement at variance with the hinge structure of the first valid type designated by Triebel (1940) as pointed out above.

The palaeontologist has only hard parts to deal with in the majority of cases, and since 1933 there has been a very considerable splitting of the genus *Cythereis* on this basis. The criteria usually used in the discrimination of species and genera are such features as hinge structure, the shape and ornamentation of the shell, the relationship between the inner margin and line of concrescence, the nature of overlap at the margins of the valves, the nature and distribution of the radial and normal pore canals, and the shape and distribution of the muscle scars. Although important biological differences may occur in the soft parts without any ascertainable differences in the hard parts, the hard parts are by no means completely divorced from the soft structures. Triebel (1941) has pointed out that the various features of the ostracod carapace do in fact bear a close relationship to the morphology of the soft parts, although Malkin (1953) considers that some of these characters may emphasize differences that are relatively insignificant biologically. The rate at which the various characters mature is variable and in her work on the Miocene, Malkin (1953, p. 777) concludes that the order of reaching the adult stage seems to be (1) shape, (2) ornamentation, (3) marginal area, (4) size and shell thickness, (5) hinge. She notes that 'the final complex hinge is the last character to mature, as would be expected, because the hinge must be relatively weak in order that the immature carapace be shed'. The dangers of dealing with immature forms in the fossil state are too well known to need re-emphasizing here.

One of the great difficulties in dealing with the Ostracoda lies in evaluating the taxonomic importance of the varying characters and in this it is particularly difficult to reconcile both zoological and palaeontological practice. On the other hand, while it has been suggested that an independent classification based on hinge structure should be set up by palaeontologists (Beroušek 1952), and that this is more or less the case in the Palaeozoic Ostracoda, such a scheme can certainly not be entertained in the case of the Mesozoic and later Ostracoda. All possible characters should be taken into account and it seems to the author that the most important of these are the nature of the first four pairs of limbs (particularly the mandible), the muscle scars, and the hinge structure. The mandible especially would seem to give a far clearer guide to the genetic relationships than the hinge and the former structure is particularly valuable in enabling a satisfactory division to be made between the Trachyleberidinae and the Hemicytherinae.

Although the hinge structure is important for distinction at the generic level, minor differences seem to have been much over-emphasized in the past and this would seem to be particularly so in the *Cytheridea* group. With further knowledge the genitalia might well prove as important as the limbs, as suggested by Skogsberg. Other features of the carapace noted above—shape, marginal areas, ornament, &c.—are all useful differentiating characters on occasion. Of these, shape, which as Malkin points out is the first feature to show adult characteristics, is the most useful in dealing with immature forms, whilst ornament is of little use at the higher taxonomic levels but is one of the most useful features at the specific level.

THE SUBFAMILY HEMICYTHERINAE

The subfamily Hemicytherinae was formed by Puri (1953) to accommodate the five genera *Hemicythere* Sars 1925, *Procythereis* Skogsberg 1928, *Caudites* Coryell and Fields 1937, *Heterocythereis* Elofson 1941, and *Urocythere* Howe 1951, which he separated

from the Trachyleberididae s.s. (= subfamily Trachyleberidinae). Puri did not discuss the differences between the Hemicytherinae and the Trachyleberidinae and the most significant statement in his diagnosis was that in the Hemicytherinae there are an 'additional three or four scars in an oblique row situated anteriorly' to the row of four adductor scars (see Pokorný 1955, p. 4, for comment on this). Subsequently Puri added the genus *Hermanites* Puri 1955 (= *Hermania* Puri 1954 preoccupied) to his original five. Pokorný (1955) reviewed the Hemicytherinae as known at the time, and for the first time gave adequate diagnoses and figures of some of the genera. As his paper was in the press he added a footnote to the effect that in the light of the new genera proposed by Hornibrook (1953) and Puri (1954) the limits between the Hemicytherinae and Trachyleberidinae were difficult to draw and that the taxonomy of the genera included in these two units needed further study. After pointing out the anomalies in Puri's original diagnosis Pokorný (1955) gave an excellent key to the genera, and, while regarding *Urocythere* as a doubtful member of the Hemicytherinae, added the genera *Urocythereis* Ruggieri 1950, *Elofsonella*, *Hemicytheria*, and *Aurila* to the subfamily.

While the present paper does not set out to give a detailed analysis of the Hemicytherinae—an impossible task until we know more about some genera—the following remarks may help to clarify the diagnosis and recognition of the subfamily. A study of the genera in which the soft parts are known shows that the subfamily Hemicytherinae Puri 1953 may be recognized as a distinct unit within the Trachyleberididae and may be most satisfactorily differentiated from the subfamily Trachyleberidinae Sylvester-Bradley 1948 on the basis of the soft parts. The soft parts are well known in *Hemicythere*, *Procythereis*, and *Heterocythereis* among Puri's original five genera, and one may single out for mention the five-jointed first antenna, the generally well-developed exopodite of the second antenna, and in particular the single plumose seta (double in the case of *Procythereis*) which forms the exopodite (= epipodial appendage of Skogsberg 1928) of the mandible. On the other hand, in *Trachyleberis* Brady 1898, *Pseudocythereis* Skogsberg 1928, and *Pterygocythereis* Blake 1933—three of the genera included by Sylvester-Bradley (1948) in the Trachyleberididae and not placed in the Hemicytherinae by Puri—the first antenna is six-jointed, the exopodite of the second antenna is much reduced, and the mandible bears a branched exopodite which consists usually of five branches. This latter would appear to provide the easiest means of differentiating between the two subfamilies when the soft parts are available for study. Using the criteria outlined above the following groupings occur:

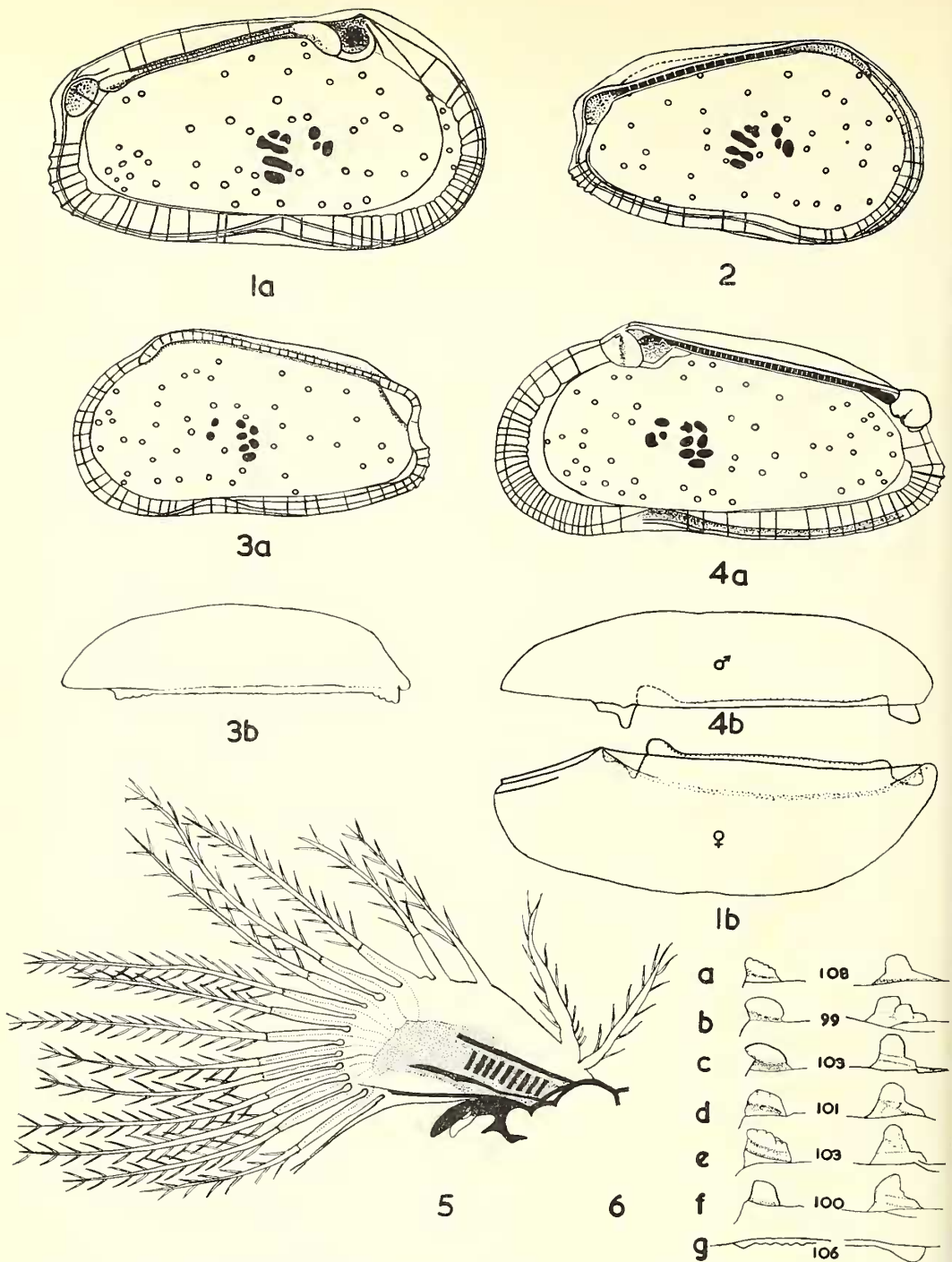
TRACHYLEBERIDINAE Sylvester-Bradley 1948.

- Trachyleberis* Brady 1898.
Pseudocythereis Skogsberg 1928.
Pterygocythereis Blake 1933.

HEMICYTHERINAE Puri 1953.

- Hemicythere* Sars 1925.
Procythereis Skogsberg 1928.
Heterocythereis Elofson 1941.
Eucythereis Klie 1940 (= *Cythereis* s.s. Skogsberg 1928 non Jones 1849 invalid).
Elofsonella Pokorný 1955 (= *Paracythereis* Elofson 1941 preoccupied).
Aurila Pokorný 1955.
Normanicythere gen. nov.

In fossil material where the limbs are not available the muscle scars give the best indication of the relationships. The main difference here lies in the muscle scars anterior



TEXT-FIG. 1. *Normanicythere leioderma* (Norman). 1, Left valve of adult female. Recent, Spitzbergen. $\times 66$. a, from inside; b, from above. R.S. 996. Dissection 6. Slide 17. 2, Left valve of immature female (penultimate instar). Recent, Spitzbergen. $\times 66$. From inside. R.S. 996. Slide 19. 3, Right valve of immature male (penultimate instar). Recent, Portree, Skye. $\times 66$. a, from inside; b, from above. H.M. 8/79. 4, Right valve of lectotype. Adult male, Unst Haaf, Shetland. $\times 66$. a, from inside b, from above. B.M. 1911.11.8.M.3210a. 5, Vibratory plate of right maxilla. Recent, Spitzbergen. $\times 195$. Composite, based on camera lucida drawings and photographs of Dissections 2 and 7. R.S. 996. Slides 2, 9, 10. 6, Variation in tooth structure of adult carapaces from Spitzbergen, seen from above. $\times 80$. a-f, right valves; g, left valve. Numbers indicate the length of the valve in hundredths of a millimetre. R.S. 996. Slide 20.

to the row of four adductor muscle scars and is probably connected with the great development of the exopodite of the second antenna and its associated antennal gland in the Hemicytherinae. In this latter subfamily the anterior field consists of two or three rounded muscle scars which lie obliquely to the vertical. In the Trachyleberidinae, on the other hand, this group of muscles is represented by one large and usually horseshoe-shaped muscle. In the vertical row of four adductor muscles there is a distinct tendency in the Hemicytherinae for the individual muscles to split into two and leave a double or 'binodal' scar, while this does not appear to occur in the Trachyleberidinae. Finally, in the Trachyleberidinae the muscle area seems to be sunk in a central pit which is not so well defined in the Hemicytherinae, although this distinction is of doubtful validity. Using the foregoing criteria one may group a number of additional genera whose soft parts are as yet unknown as follows:

TRACHYLEBERIDINAE

Cythereis Jones 1849.*Buntonia* Howe 1935.*Isocythereis* Triebel 1940.*Platycythereis* Triebel 1940.*Oligocythereis* Sylvester-Bradley 1948

HEMICYTHERINAE

Urocythereis Ruggieri 1950.*Tyrrhenocythere* Ruggieri 1955.*Hemicytheria* Pokorný 1955.

Although a number of genera placed in the Trachyleberididae cannot at the present time be placed in their respective subfamilies due to inadequate information on their soft parts or muscle scar pattern, it is suggested that the essential differences between the Trachyleberidinae and the Hemicytherinae lie in the features outlined above, rather than in any general consideration of shape, hinge or ornament.

SYSTEMATIC DESCRIPTION

Family TRACHYLEBERIDIDAE Sylvester-Bradley 1948

Subfamily HEMICYTHERINAE Puri 1953

Revised Diagnosis. Trachyleberididae which differ from the Trachyleberidinae in having a five-jointed first antenna, the second antenna with well-developed exopodite, and the exopodite of the mandible formed of a single (or occasionally double) plumose seta. The muscle-scar pattern differs from that in the Trachyleberidinae in that there are two or three scars in an oblique row anterior to the adductor muscles, and the latter tend to be binodal.

Genus *Normanicythere* gen. nov.Type Species *Cythere leioderma* Norman 1869

Diagnosis. Third endopodite of the distinctive mandible with seven antero-distal setae and one large postero-distal seta, the latter being smooth proximally and serrate distally and carrying six long hair-like processes. Adult hinge amphidont with stirpate anterior tooth. Posterior tooth usually reniform. Hinge line straight and oblique to dorsal margin of the shell seen from the side. Inner margin and line of concrescence well separated anteriorly and at postero-ventral angle. Radial pore canals simple.

Normanicythere leioderma (Norman)

Plates 13, 14

Cythere leioderma, n.sp.; Norman 1869, pp. 255, 291.*Cythere leioderma*, Norman; Brady 1870, pp. 451-2, pl. 19, figs. 11-13.*Cythere leioderma* (Norman); Brady and Crosskey 1871, pp. 61-2.*Cythere leioderma*, Norman; Brady, Crosskey, and Robertson 1874, pp. 149, 150, pl. 9, figs. 5, 6.*Cythere leioderma*, Norman; Brady 1878, p. 254.*Cythere leioderma*, Norman; Brady and Norman 1889, p. 139, pl. 15, figs. 12, 13.*Cythere leioderma*, Norman; Norman 1891, p. 111.*Cythere leioderma* Norm.; Müller 1912, p. 377.*Cythere leioderma*, Norman; Stephensen 1913, p. 363.*Cythere leioderma* A. M. Norman; Klie 1929, pp. 19, 42.*Cythere* (?) *leioderma* Norman; Müller 1931, p. 30.*Cythereis leioderma* (Norman) comb. nov.; Blake 1933, p. 239.*Cythereis leioderma* (Norman); Stephensen 1938, pp. 10, 17.*Cythereis* (?) *leioderma* (Norman); Elofson 1941, p. 304.*nonCythere leioderma*, Norman; Seguenza 1884, p. 51.

Types. Nine syntypes in the British Museum (Natural History), London, nos. 1911.11.8.M.3210*a-i*, from Unst Haaf, Shetland. Of these, an adult male, right valve, no. 1911.11.8.M.3210*a* is here chosen as the lectotype.

Description

(a) *The Carapace.* In lateral view the shape is an elongate oblong, rounded anteriorly with straight dorsal margin and almost straight or slightly sinuate ventral margin. The

EXPLANATION OF PLATE 13

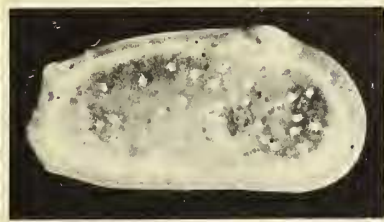
Figs. 1, 2, *Normanicythere leioderma* (Norman), Recent, Spitzbergen. 1, Adult female seen from the left with all the right side limbs removed. $\times 115$. ag.—antennal gland; 1*a*, first antenna; 2*a*, second antenna; ex.—exopodite ('Spinnborste'); mdp.—mandibular palp; mx.—maxilla; 1wl, 2wl, 3wl.—first, second, and third walking legs; fs.—furcal setae; ts.—terminal seta. R.S. 996. Dissection 4, Slide 4. 2, Male genitalia seen from the front. $\times 165$. mcs.—median chitinous support; pe.—penis; co.—copulatory organ; ode.—opening of ductus ejaculatorius; rc.—rounded corner of co.; fl.—flagella; de.—ductus ejaculatorius; 1fs, 2fs, 3fs.—first, second, and third furcal setae. R.S. 996. Dissection 2, Slide 2.

EXPLANATION OF PLATE 14

Figs. 1-8, *Normanicythere leioderma* (Norman), $\times 42$. 1, Lectotype. Adult male. Right valve. Recent, Unst Haaf, Shetland; (a) outside, (b) inside, (c) dorsal view. B.M. 1911.11.8.M.3210*a*. 2, Syntype. Adult female carapace. Recent, Unst Haaf, Shetland; (a) from left, (b) from right, (c) dorsal view. B.M. 1911.11.8.M.3210*b*. 3, Adult male. Right valve. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (a) outside, (b) inside, (c) dorsal view. H.U. 1.Q.1.1. 4, Syntype. Immature female. Left valve. Penultimate instar. Recent, Unst Haaf, Shetland; (a) outside, (b) dorsal view. B.M. 1911.11.8.M.3210*c*. 5, Syntype. Immature female. Right valve. Recent, Unst Haaf, Shetland; (a) outside, (b) dorsal view. B.M. 1911.11.8.M.3210*d*. 6, Immature female. Left valve. Penultimate instar. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (a) outside, (b) inside, (c) dorsal view. H.U. 1.Q.1.2. 7, Immature female. Right valve. Penultimate instar. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (a) outside, (b) inside, (c) dorsal view. H.U. 1.Q.1.3. 8, Immature carapace. Instar 5. Recent, Spitzbergen. (a) from left, (b) dorsal view. R.S. 996. Slide 21.



NEALE, *Normanicythere leioderma* (Norman)



1a



1b



1c



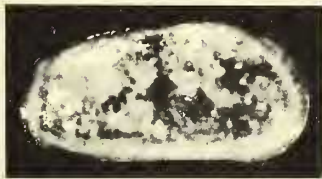
2c



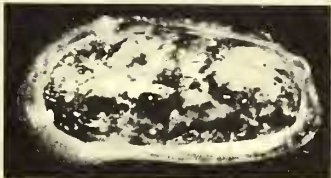
2a



2b



3a



3b



3c



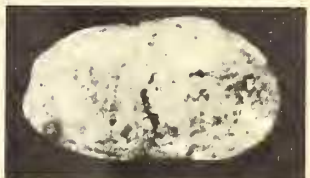
4b



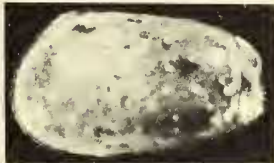
5b



4a



5a



6a



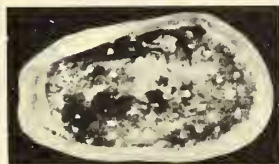
6c



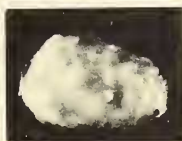
7c



7a



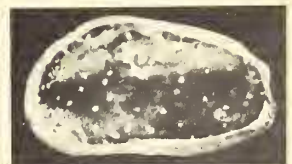
6b



8a



8b



7b

posterior margin is truncate or sinuate, the sinuation being due largely to the development of the strongly everted posterior tooth in the right valve with its corresponding socket in the left. The carapace is highest anteriorly and the left valve is slightly larger than the right valve, overlapping the latter in the region of the anterior tooth. The greatest height is a little more than half the length and sexual dimorphism is pronounced in the adult, and to a lesser extent in the penultimate instar, the females being higher in proportion to the length than the males (text-fig. 1, figs. 1*a*, 4*a*; Pl. 14). The dorsal hinge line is straight, the shell gradually rising above it posteriorly to form a shallow trough which is deepest at the posterior end. In dorsal view the carapace is more or less evenly rounded with a suggestion of a vertical median sulcus, and is rather parallel-sided in the case of the male, and somewhat pear-shaped and widest posteriorly in the case of the female. In this view the tooth structure (q.v.) is very characteristic (text-fig. 1, figs. 1*b*, 4*b*). The carapace is smooth and unornamented.

In immature forms the line of concrescence and inner margin coincide except at the postero-ventral angle. In the adult the line of concrescence and inner margin are very near or coincident ventrally, but are well separated anteriorly and at the postero-ventral angle. Radial pore canals, which are simple and usually well marked, are densest at the antero-ventral border and postero-ventral angle in which latter position there may be a slightly serrate margin to the carapace (*randzähnen*). Antero-dorsally and ventrally the radial pore canals are more sparsely distributed. The normal pore canals are large, very distinct and well spaced, appearing as lucid spots under the microscope and sometimes giving the impression of raised papillae (Pl. 14, figs. 1*a*, 7*a*). In immature and thin-shelled specimens these canals are easily seen, but are much less easily seen in the case of some older or thick-shelled specimens. The selvage is well developed in both immature and mature forms and ventrally the left valve fits into a groove in the right valve, the latter overlapping the left valve along the posterior part of the ventral margin. Anteriorly the relative overlap is reversed and the left valve overlaps the right.

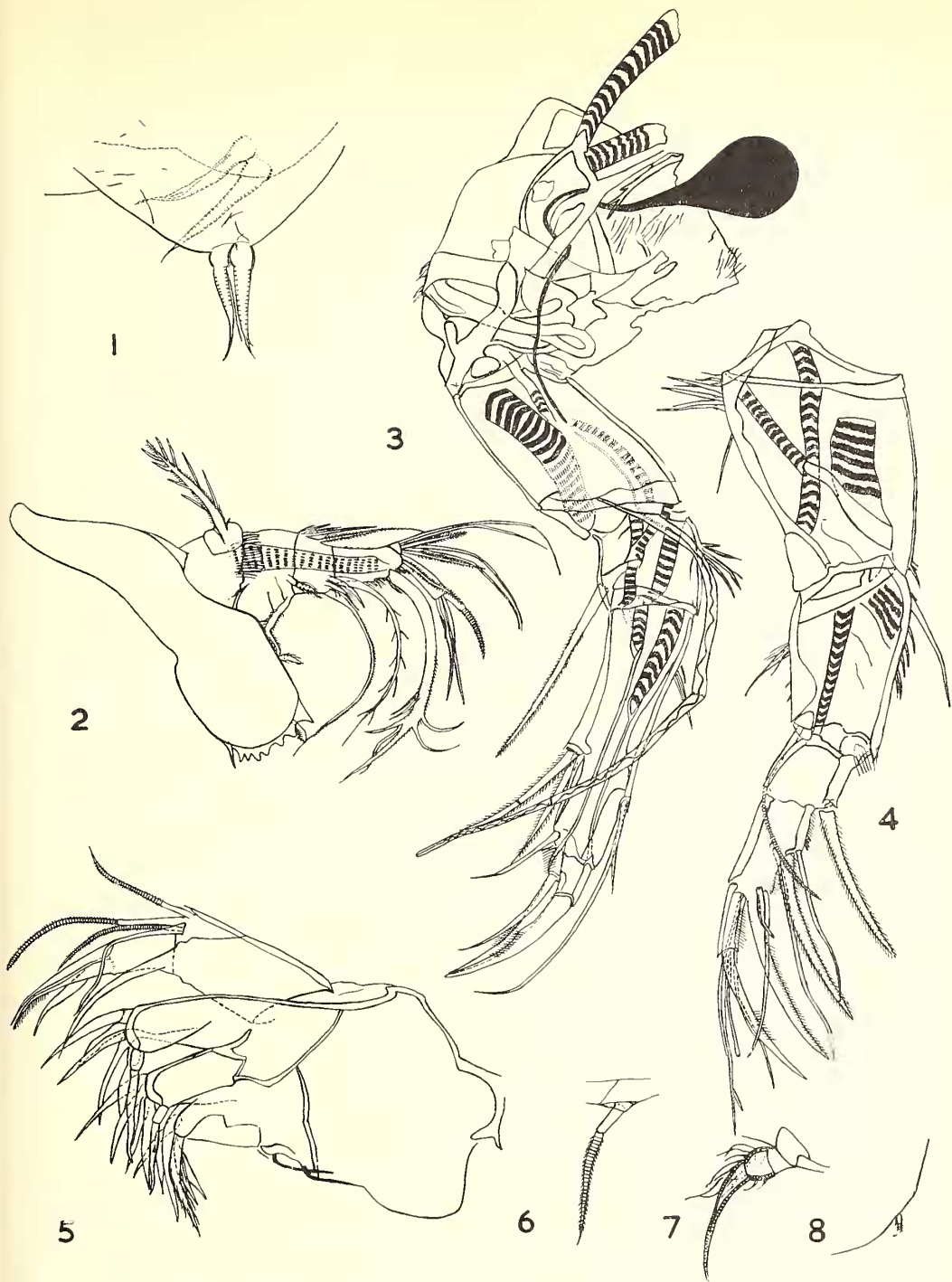
The muscle-scar pattern consists basically of a vertical row of four adductor scars with three muscle scars anterior to, and on a level with, the two more dorsally situated scars of the row of four. In the adult two or three small scars are sometimes seen about the same distance above the row of four scars as the height of the row. There is some minor variation in the adult pattern but in the row of four scars: 1, the bottom scar is always single; 2, the ventral central scar is very elongated and narrow and tends to be 'binodal' or form a double scar; 3, the dorsal central scar is not so elongate and is generally binodal; 4, the dorsal scar is a double scar in the adult. In immature specimens the muscle pattern is similar but the scars are more rounded and less elongated. In the adult there are three rounded equidimensional muscles in an oblique row anterior to the vertical row of four. The dorsal and ventral of these are easily seen, the smaller median one less so.

The hinge structure shows a big change from merodont in the penultimate instar to amphidont in the adult (see Sylvester-Bradley 1956 for terminology). The right valve of the penultimate instar (text-fig. 1, fig. 3*a*) has an anterior and posterior tooth joined by a finely denticulate bar, with a groove or shelf below which is open ventrally. The anterior tooth is triangular in dorsal view (Pl. 14, figs. 5*b*, 7*c*), highest anteriorly and in strongly oblique lighting shows a subdivision into three or four crenulations. The posterior tooth is a deep, plate-like, outstanding tooth formed by the everted posterior

angle of the right valve. This too shows a subdivision into four or five distinct crenulations. The inseting of the tooth at the posterior corner of the valve gives a very characteristic appearance, especially when viewed from dorsally. The left valve (text-fig. 1, fig. 2; Pl. 14, figs. 6a-c) overlaps the right along the hinge margin. The hinge consists of a deep posterior socket, a locellate groove which accommodates the marginal bar of the right valve, and a shallow socket anteriorly for the anterior tooth. Anteriorly the valve has a curiously unfinished look due to this rather ill-defined socket. In the adult hinge the right valve has a large, stirpate anterior tooth with post-jacent socket and faintly locellate groove, the latter being defined above and below by a thin ridge or bar. Posteriorly is a large outstanding tooth which markedly affects the outline of the shell. This tooth is rather rhomb-shaped in the lectotype but reniform in the adult male from Dimlington (Pl. 14, fig. 3b). Some of the variations in shape of these teeth in the Spitsbergen material are shown in text-fig. 1, fig. 6. Posteriorly the dorsal bar and groove are slightly modified immediately anterior to the posterior tooth. The bar (which may be faintly denticulate) shows two small crenulations or vestigial teeth which seem to be a relic of the previous instar tooth pattern, while the groove is somewhat enlarged to form a small socket into which fits a complementary expansion of the bar in the left valve. In the left valve the anterior socket shows minor variations in shape corresponding to those seen in the anterior tooth in the right valve, and is succeeded posteriorly by a large tooth and faintly denticulate bar. These denticulations are best seen posteriorly before the slight expansion of the bar to form the posterior tooth (text-fig. 1, figs. 1b, 6g). A deep socket to accommodate the posterior tooth completes the hinge.

(b) *The limbs and soft parts.* Five dissections (three female, two male) and two partial dissections were made and all the line figures were drawn by camera lucida at magnifications of either 390 or 780. These figures were then checked by examination with an oil-immersion lens at $\times 1,000$ when minor details of pilosity and pectination were added freehand. The most recent detailed description of an advanced marine Podocopa is due to Harding (Harding and Sylvester-Bradley 1953) and the terminology used below follows that paper closely. In the present description, however, 'inside' is used in preference to 'median' in referring to the inside surface of the leg, and median is restricted to describing structures occurring on the mid-line of the body. Proportional lengths are not given for the various segments (numbered from proximally to distally) and for these reference should be made to the appropriate figures. As the annulate setae carry hairs at each joint or annulus these are not referred to as hairy in the text but are shown on the figures. All the limbs are bilaterally symmetrical and the absence of any comment on sexual dimorphism indicates that a particular limb is the same in both sexes.

The first antenna consists of five segments. Segment 1 carries a tuft of long spinules on the posterior face near the base, and small spinules at the antero-distal corner. Segment 2 has tufts of spinules both anteriorly and posteriorly. One or two of these spinules are more prominent than the rest. The more prominent spinules anteriorly lie in the proximal position, while posteriorly the most prominent lie about half-way down the segment. A tuft of fine spinules and hairs lies anterodistally and there is a slender, flexible, annulate seta at the postero-distal corner. Segment 3 has a single major seta, which is pectinate on both sides, at the antero-distal corner. Segment 4 corresponds to segments 4 and 5 in *Trachyleberis* and *Pseudocythereis* but shows continuous chitinization posteriorly in which it agrees with *Hemicythere* and *Cythereis* s.s. (*sensu* Skogsberg). It carries two



TEXT-FIG. 2. *Normanicythere leioderma* (Norman). Recent, Spitzbergen. 1, Furcal setae seen from the left-hand side. Female. $\times 390$. R.S. 996 Dissection 4, Slide 4. 2, Right mandible from outside. Male. $\times 195$. R.S. 996. Dissection 2, Slide 2. 3, Right second antenna from outside. Male. $\times 195$. R.S. 996. Dissection 2, Slide 2. 4, Right first antenna from outside, Male. $\times 195$. R.S. 996. Dissection 2. Slide 2. 5, Left maxillary palp and endites from outside. Male. $\times 390$. R.S. 996. Dissection 5, Slide 5. 6, Postero-proximal seta. Third right walking leg (seventh limb). Female. $\times 390$. R.S. 996. Dissection 6, Slide 7. 7, Postero-proximal seta of first right walking leg (fifth limb). Female. $\times 390$. R.S. 996. Dissection 6, Slide 7. 8, Median terminal seta. Female. $\times 390$, seen from left. R.S. 996. Dissection 4, Slide 4.

stout major setae—one antero-median in position, the other antero-distal. The former, which is pectinate on both sides, is associated with two more slender, bristle-like setae—one as long as the major seta lying more posteriorly on the inside of the limb; the other, somewhat shorter, lying above (i.e. proximal to) the main seta. The distal seta, which is pectinate on the anterior side only, is also associated with two bristle-like setae, the longer one again placed on the inside of the limb in a more posterior position, the shorter one again lying above the main seta. In addition there is a very short seta, which is at first cylindrical and then tapers rapidly, placed distally on the outside of the limb (latero-distal spine of Skogsberg 1928, p. 40.). This segment is finely pilose anteriorly. Segment 5 shows a somewhat similar pattern with a single major, distal seta, two bristle-like setae and in addition a somewhat shorter sense club. The middle third of the major seta is pectinate on the anterior side, carrying about ten or eleven hairs, but this is only seen with great difficulty and some specimens appear smooth. It appears to be more obvious in the males than the females. This segment is finely pilose anteriorly.

The second antenna shows distinct sexual dimorphism in the case of the long bristle-like seta on the anterior side of the second endopodite segment. The protopodite of one segment is followed by an endopodite of three segments and a long, slender exopodite, also of three segments.

Endopodite 1 is short with a tuft of spinules anteriorly about the middle of the segment and a hairy seta at the postero-distal corner. Endopodite 2 is much elongated and carries a patch of spinules on the anterior side about a quarter of the way down from the proximal end. This segment has two hairy setae posteriorly about two-thirds of the way down, associated with a rather shorter sense club which lies immediately anterior to them on the outer side of the limb. Immediately above these setae the surface has a number of short fine hairs. Anteriorly about three-quarters of the way down the segment are two bristle-like setae. The inner, shorter one reaches to about the middle of the last segment while the outer, longer seta extends level with the distal tip of the terminal seta. In the female this longer seta only reaches about half-way down the terminal seta. There is a short pilose seta at the postero-distal corner with a fringe of hairs lying anterior to it. Endopodite 3 has two setae half-way down the posterior side, a stouter one which is pectinate, carrying about a dozen hairs on the middle third of the posterior (upper) surface and occupying the inner position; the other more slender one lying outside it. There is a stout, terminal seta which is also pectinate in the middle third of the upper surface, carrying eleven or twelve hairs. Skogsberg (1928, p. 44) remarks that in *Cythereis* the distal claws of the female are more strongly pectinate than those in the male. There is some slight suggestion of this in the present species.

The exopodite (*Spinborste* of Müller, Klie, &c.) contains the efferent duct for the large gland (*Spinndrüse*) which lies on either side of the body near the base of the second antenna (Pl. 13, fig. 1. *ag.*, text-fig. 2, fig. 3). This gland appears to be best developed in those marine *Cytheracea* living among seaweeds and large detritus and is much reduced in many of the mud dwelling forms according to Elofson (1941, p. 438). The function of the gland appears to be that of spinning a thread which functions as a climbing or safety rope and Elofson goes on to state 'Oft habe ich in Aquarien beobachtet, wie Individuen einer Anzahl Algenarten (*Cytherura*, *Loxoconcha*-Larven) von ihrem Zweig herunterfielen, aber an den Spinnfäden hängen blieben und wie Spinnen wieder an diesen hinaufkletterten.'

The mandible consists of a strongly chitinized *pars incisiva* and an attached mandibular palp shown in text-fig. 2. The biting edge consists of a row of six main teeth, of which the anterior two are by far the strongest, with a row of six more, slightly less prominent teeth, lying outside it. Between the first two teeth is a bifurcate seta about twice the length of the largest tooth, each arm of the seta being armed with small, fine hairs on the posterior side. In addition there is a small, smooth, tapered seta at the postero-ventral corner, and a hairy, rather carrot-shaped seta on the anterior side of the body of the mandible.

The mandibular palp consists of a protopodite of one segment, which together with an exopodite of one segment is well chitinized, and an endopodite of four segments which is very poorly chitinized except for the most distal segment, segmentation often being difficult to observe in the first three segments. The protopodite carries a series of long hairs along the distal margin. The exopodite carries a single pilose seta which has, in addition, some four pairs of longer hairs. Endopodite 1 has a slender seta posteriorly which is pilose on both sides and has, lying dorsal to it, a hairy seta which shows signs of annulation. Endopodite 2 has two dorsal setae. The proximal is really the largest of a group of four spinules which increase in size distally, while the distal one is annulate. Ventrally there are two long, slender setae lying outside which, near their bases, are two small setae. The inner long seta is minutely pilose on the anterior edge, while the outer long seta is armed with five pairs of rather long hairs. Of the two small setae, the more ventral is a little shorter and more hairy than the dorsal. Endopodite 3 has a few small hairs on the dorsal surface and a felt of long hairs on the ventral. Antero-distally this segment has a bundle of seven setae—four, distributed in two pairs, very long, smooth, and whip-like; the other three, which are about half the length of the latter are pilose on both sides. Postero-distally (ventrally) is the largest seta of the palp which has a short, smooth, slender seta at its base on the outside. The large seta is smooth proximally but is serrate and pectinate for the distal half of the anterior side, and the distal third of the posterior side. There are six long, hair-like processes of which two are placed on the posterior side some distance proximal to the others, which latter often assume a grapnel-like position when mounted.

Endopodite 4 has four distal setae, the antero-distal one annulate, the postero-distal one smooth being cylindrical at first and then tapering rapidly; while the other two setae are about twice as long and are smooth anteriorly and minutely pilose posteriorly.

The maxilla consists of a vibratory plate and palp with associated endites. The vibratory plate has eighteen plumose setae whose distribution is figured in text-fig. 1, fig. 5, and which it is unnecessary to describe further. Anterior to this is a palp and three associated endites (text-fig. 2, fig. 5). The palp consists of two cylindrical segments, the first being about twice as long and wide as the second. On the distal edge of the first segment, dorsal to the second segment are three slender annulate setae, the longest of them placed centrally and towards the outside. There is an associated fourth flagella-like, non-annulate seta which is outside, and slightly ventral to, the main annulate seta. Ventral of the second segment, a fifth stout, smooth, curved seta is placed at the ventero-distal corner. The second segment carries three setae—a smooth antero-distal blade-like seta, and two setae postero-distally—the inner one like the latter, the outer one slightly larger and pectinate on the posterior (ventral) side.

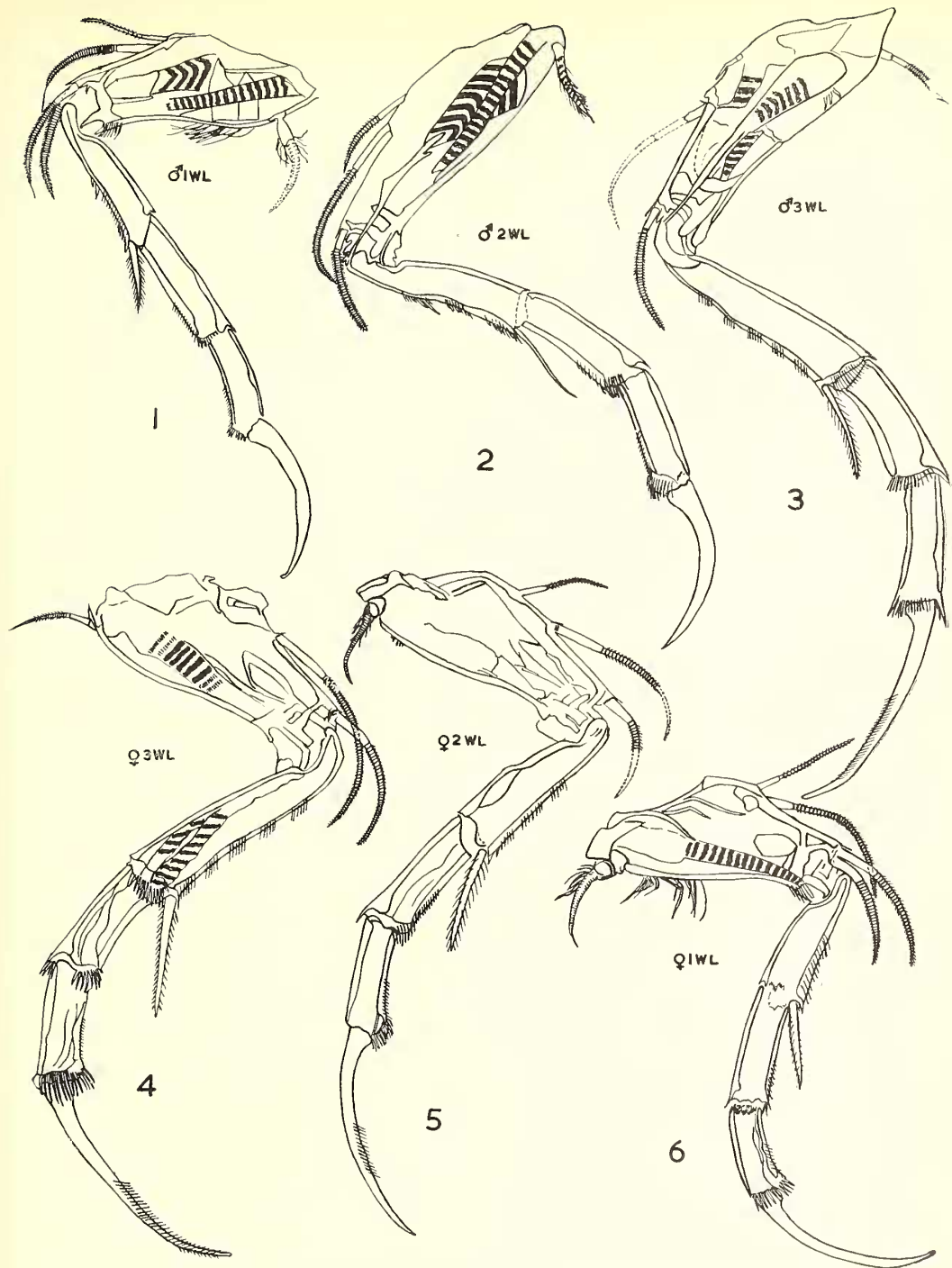
Endite 1 nearest the palp carries six smooth, rather similar, tapering setae disposed

in an outer and an inner row of three each. Endite 2 is similar, while Endite 3 appears to have seven setae, with, in addition, a larger hairy seta on the outside of the endite.

The first walking leg (fifth limb) (text-fig. 3, figs. 1, 6). Special attention was paid to this leg in view of Harding's remarks on the same leg in *Trachyleberis* but no asymmetry or significant sexual dimorphism could be detected. The leg consists of four segments. Segment 1 has two annulate setae on the anterior margin and two on the antero-distal corner overhanging the 'knee'. The posterior side has a felt of long hairs and spinules and distally there is a hollow with a fringe of hairs. Patches of hairs occur on the outside of this segment particularly in the proximal half and near the base on the posterior side is a hairy, carrot-shaped seta (text-fig. 2, fig. 7). Segment 2 broadens distally and has one non-annulate, hairy seta antero-distally. This occupies the same position in male and female with a tendency to be a little more pilose in the male. The distal two-thirds of the segment has small hairs anteriorly, a patch about the middle of the anterior edge being slightly larger than the rest in both sexes. The third and fourth segments are similar, the distal half of the anterior edge having fine hairs, while antero-distally a fringe of hairs, which shows a slight tendency to be better developed in the female, overhangs the next segment or seta. Distally the fourth segment carries a curved claw or seta which is smooth in both sexes.

The second walking leg (sixth limb) shows marked sexual dimorphism (text-fig. 3, figs. 2, 5). The first segment is similar in both sexes and has two annulate setae on the anterior side whilst a further annulate seta overhangs the 'knee'. At the postero-proximal corner there is a hairy, carrot-like seta which tends to be rather stumper in the female than in the male, and there is a spinule at the base of the limb in the middle of the outside surface. The second segment broadens distally and has three patches of hairs on the anterior side, the middle patch being the most prominent. The antero-distal corner has a seta which is long, smooth and slender in the male, and more robust and hairy in the female. Segments 3 and 4 carry a number of fine hairs on the distal half of their anterior sides and overhanging the following segment or terminal claw are fringes of hairs which are more prominent in the female than the male. The terminal claw or seta is curved and is longer and more slender in the female than the male. In the male this seta is smooth, while in the female it is pectinate for the middle third of its length on the anterior side where it carries between six and twenty hairs.

The third walking leg (seventh limb) consists of four segments and shows only slight sexual dimorphism (text-fig. 3, figs. 3, 4). The first segment carries a very small seta proximally on the anterior edge and two annulate setae—one midway along the segment and the other overhanging the 'knee'. At the postero-proximal corner there is a slender annulate seta (text-fig. 2, fig. 6), and a few small spinules may occur proximally on the outer surface near the posterior edge. The second segment broadens distally and has five patches of hairs anteriorly, which are more conspicuous in the female than the male. There is a pilose antero-distal non-annulate seta which is rather slimmer in the males than the females. A fringe of hairs occurs distally. Segments 3 and 4 are similar and have a fringe of hairs distally which is again rather more prominent in the females than the males. The terminal claw is long, narrow, and pectinate on the inside curve in its distal half. Pectination is also present on the posterior distal sixth of the claw, although difficult to see in the males. In the female the claw tends to be more incurved distally than in the male.



TEXT-FIG 3. *Normanicythere leioderma* (Norman), Recent, Spitzbergen. All figures $\times 195$. 1, First left walking leg (fifth limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 2, Second left walking leg (sixth limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 3, Third left walking leg (seventh limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 4, Third right walking leg (seventh limb) from outside. Female. R.S. 996. Dissection 6, Slide 7. 5, Second right walking leg (sixth limb) from outside. Female. R.S. 996. Dissection 6, Slide 7. 6, First right walking leg (fifth limb) from outside. Female. R.S. 996. Dissection 6, Slide 7.

The genitalia are extremely complex. It appears to the author that some of the terminology needs revision but for the present purpose that of Skogsberg (1928) has been adopted. In the male (Pl. 13, fig. 2) the genitalia consist of a median chitinized supporting structure (*mcs*) with heavily chitinized paired organs on either side. These paired organs consist of two parts—a somewhat oval muscular ‘penis’ (*pe*) and a distal triangular ‘copulatory appendage’ (*co*). The muscular part has a number of chitinous structures which stain heavily. There is a spiral *ductus ejaculatorius* (*de*) which runs from a heavily stained chamber and opens ventrally in a brush-like organ (*ode*) towards the rear of the copulatory appendage. More posteriorly is a two-fingered flagellum (*fl*) and the postero-ventral corner of the appendage is rounded (*rc*). The *vasa deferentia* could not be ascertained. Associated with the genitalia are three pairs of furcal setae—two pairs of which are relatively large, hairy, and carrot-shaped (*fs2*, *fs3*), the third pair (*fs1*) being only a third the length of the others but also armed with hairs. The paired penes were symmetrical and showed no trace of the asymmetry described by Skogsberg in certain species of ‘*Cythereis*’ and Triebel (1956) in *Xestoleberis arcturi*.

The female genitalia did not take stain and were only imperfectly seen and so will not be described. The female differs in that only the two pairs of more prominent furcal setae are developed (text-fig. 1) the small pair (*fs1*) being absent.

Brush-like organs, which generally occur in the male on the ventral side of the body near the fifth pair of limbs were not seen.

The body ends in a minute median, terminal seta (Pl. 13, fig. 1, *ts*).

Affinities and differences

The soft parts are most distinctive and show that the genus is most closely akin to *Heterocythereis* Elofson 1941 (type species *Cythere albomaculata* Baird 1850) and somewhat less closely related to *Elofsonella* Pokorný 1955 (type species *Cythere concinna* Jones 1856). In *Normanicythere* and *Heterocythereis* the first and second antennae are identical to all intents and purposes, and it is only in the mandible that differences occur. We are dependant on Sars’s figure (1925, pl. 78, fig. 1*M*) for the nature of this latter in *Heterocythereis* and he does not describe the limb in any detail. The mandibles in the two genera show an obvious general similarity, particularly in the fact that ‘the inner distal seta of the penultimate joint [is] remarkably strong and falciform curved’ (Sars, p. 169). There are, however, important differences. The distal annulate seta of Endopodite 2 is missing in Sars’s figured specimen (probably broken off), while the antero-distal margin of Endopodite 3 carries five long setae in *H. albomaculata* as compared with four long whip-like and three shorter pilose setae in *Normanicythere*. Postero-distally on this segment the main seta also carries six longer hairs which are absent in *Heterocythereis*. The distal segment in the latter genus also carries three instead of four setae, and there are also marked differences in pilosity on the two posterior setae of Endopodite 2. While it is obvious that *Normanicythere* is closely related to *Heterocythereis*, it is equally obvious that there are differences in the structural details and that the soft parts of *Heterocythereis albomaculata* need careful re-examination and redescription. In the hard parts, these two genera differ considerably. Wagner (1957, pl. 24) gives the best figure of the carapace of *Heterocythereis* and while in this genus the hinge follows the arched dorsal margin, in *Normanicythere* the hinge is straight and

sinks below the margin of the shell posteriorly. In addition the detailed hinge structure, the marginal areas, and the distribution of the radial pore canals is different. There is, however, a similarity in the large normal pore canals which again suggests a fairly close kinship.

From *Elofsonella* the differences are more marked, both in the antennae—the exopodite of the second antenna is much reduced in *Elofsonella* for example—and in the mandible where the postero-distal seta is less developed.

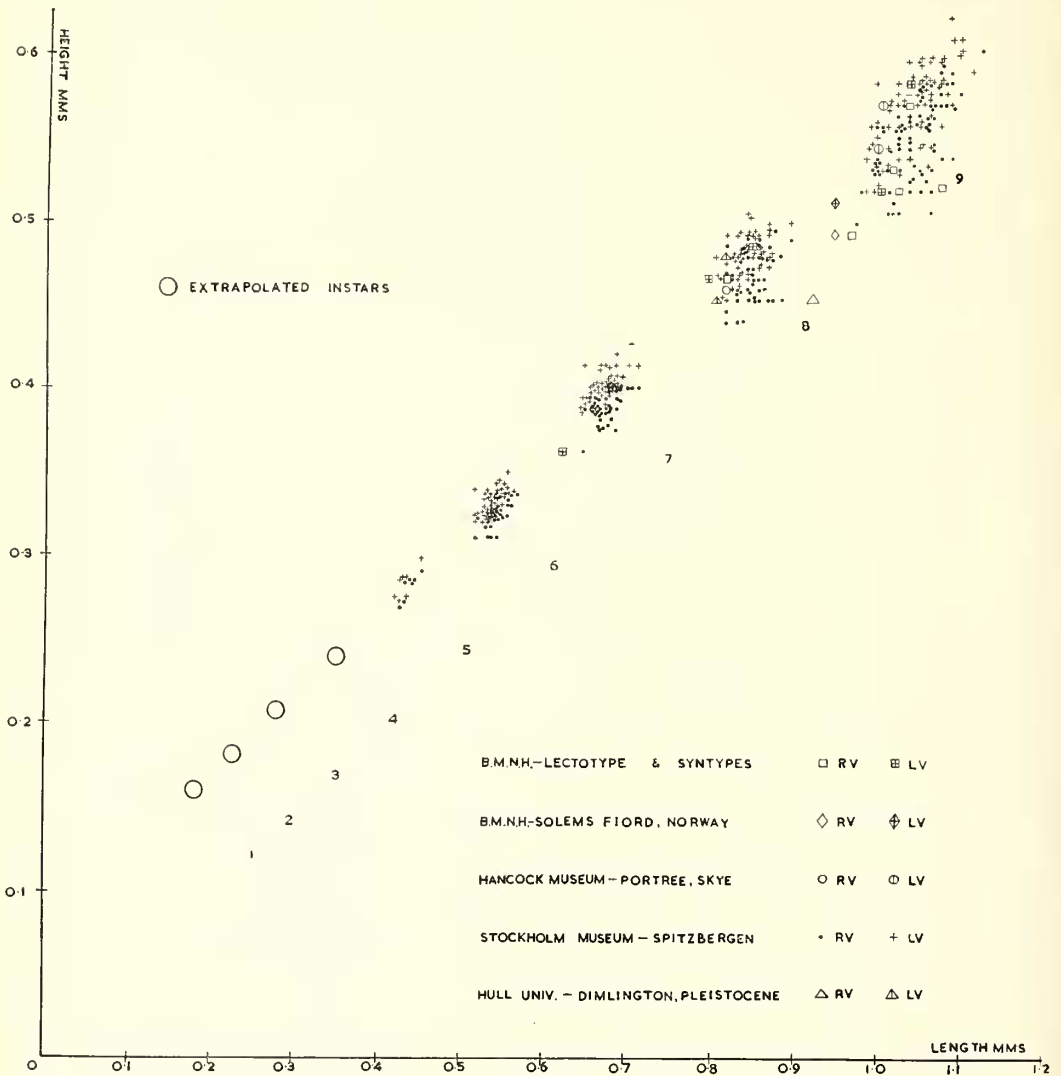
The hard parts differ markedly from many of the genera placed in the Trachyleberididae and a list would be tedious. The present genus is closest to *Campylocythere*, *Elofsonella*, and *Urocythereis*. While *Normanicythere* agrees with the description of *Campylocythere* (= *Acuticythereis*) Edwards (1944, p. 514) there are striking differences in the hinge structure compared with Edwards's figures (1944, pl. 86, figs. 8–16) and in the soft parts as far as they are known. This is particularly so in the case of the first antenna (= antennule) as figured by Swain (1955, text-fig. 39, fig. 8*b*) in *C. concinnoidea* (not the type species) which has only three endopodite segments instead of four and differs markedly in the setae also. From *Urocythereis* Ruggieri 1950 it differs in the development of the hinge and particularly in the vestibule developed anteriorly and the separation of the inner margin and the line of concrescence at the postero-ventral angle. The differences in the hard parts from those of *Elofsonella* are not so well marked and lie in the inseting of the hinge and the large scattered pore canals of the new genus, the differences being much more marked in the case of the soft parts.

Growth

Growth shows the usual discontinuous pattern associated with Ostracoda and other Crustacea. Ecdysis occurs periodically and is accompanied by a rapid increase in size when a new and larger carapace is formed. There follows a period during which size remains stable (the instar) until ecdysis recurs. Two 'laws' have been postulated to explain the size relationships between instars in this discontinuous type of growth. Brooks (1886) working on the Stomatopoda suggested that there was a constant percentage increase in length of the carapace at each moult, a concept first applied to the Ostracoda by Fowler (1909); and Przi Bram (1931) working with weight and volume suggested that the volume of the shell roughly doubled after ecdysis. Later work has upheld the general validity of these hypotheses and the position has been summarized by Kesling (1953).

All available specimens of *N. leioderma*, including both left and right valves in complete specimens, were measured and the results were plotted in a simple height: length graph (text-fig. 4). Four hundred and one valves from Spitsbergen were measured and showed the presence of five instars including the final adult stage, disposed in an extremely compact pattern indicating a single interbreeding community. Material from other localities in some cases falls within the size limits of Spitsbergen instars, and in others well outside. This seems to indicate that communities of one species in different localities may have different absolute measurements with regard to a particular instar and that the result of plotting more equal numbers of specimens from different localities would be to blur the sharpness of the graph. By taking the modes of the various instars it is possible to calculate the average increase in length from instar 5 to the adult, this increase being successively 1.254, 1.238, 1.247, and 1.239. The constancy of these values

is enough to indicate the general truth of Brooks's Law in respect of this species. The average value for the increase in size at ecdysis is 1.2445 and this figure was used to work out the hypothetical early instar sizes shown in text-fig. 4. It differs slightly from the generalized value of 1.25992 given by Kesling (1953, p. 105).



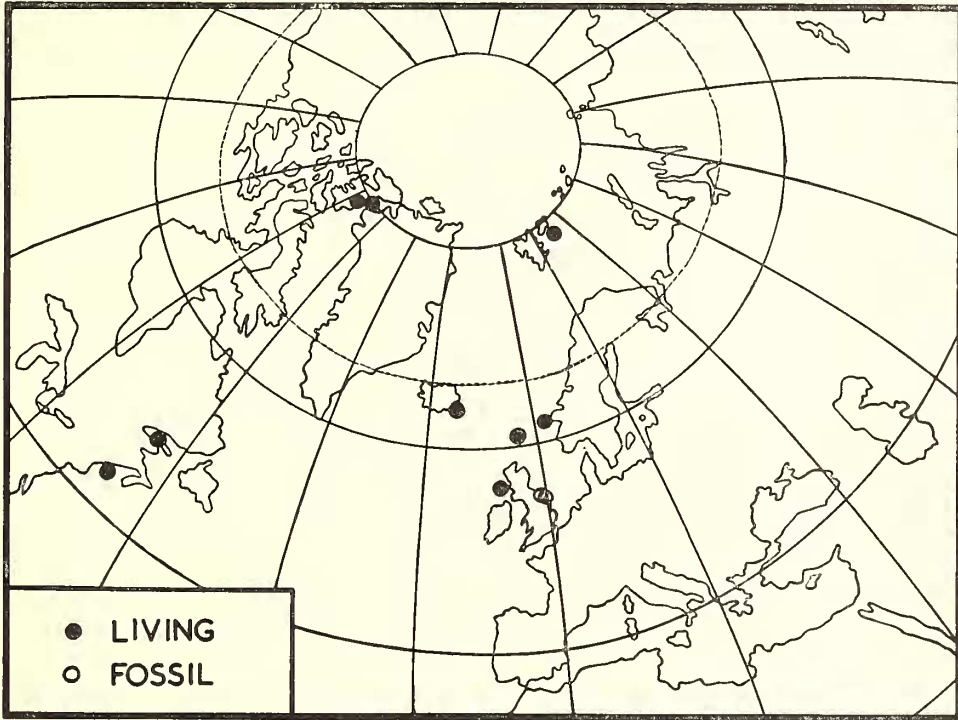
TEXT-FIG. 4. Graph showing the size distribution of carapaces in *N. leioderma*.

It is suggested on text-fig. 4 that altogether there are nine instars in the full life span of *Normaniclythere leioderma*. Obviously this conclusion is tentative and can only be verified by breeding living material. There is little data to indicate the average size of the first instar in closely related forms but the value of about 0.18 mm. length postulated here is not inconsistent with the figures given by Elofson (1941, p. 378) for such forms as *Cythere lutea* (0.156 mm.) and *Cyprideis littoralis* (0.150 mm.).

In *N. leioderma*, due to its shape, the volume $\simeq \frac{1}{2}$ length \times height²; and when the values obtained by using this formula are plotted graphically (graph not shown here) there is a close approximation to the curve $V_2 = 2V_1$ (Przibram's Law).

Distribution

N. leioderma is characteristic of marine conditions and Elofson (1941) has recorded that it is unknown where the salinity falls below 26 to 30 parts per thousand. Its distribution (text-fig. 5) shows it to be an essentially cold-water species, and as early as



TEXT-FIG. 5. Distribution of *Normanicythere leioderma* (Norman).

1891 Norman (p. 120) included it in his list of Arctic species. The living form occurs rather rarely on the eastern side of the Atlantic. Norman (1869) obtained nine specimens (the type material) from 'very deep water' in Unst Haaf, Shetland; and a single specimen (also in the British Museum) from 50 to 60 fathoms in Solems Fiord, Norway (Brady and Norman 1889, p. 111). Norman (1891, p. 111) further localizes this latter as 'Flöro'. A search of the 1:200,000 Ampt maps of Norway revealed no Solems Fiord. There is in fact no Sulen Fjord shown, but Sulen on the north side of Sognesjøen lies just north of Flöro and presumably Norman's locality is in its vicinity. Elofson only found this species at one station in the Skaggerak ($58^{\circ} 18' N. 10^{\circ} 49.5' E.$), where he obtained four valves. Hitherto this has been thought to be its southern limit on this side of the Atlantic, but three specimens (mature male and female left valves, and an